

ROLE SPECIALIZATION IN THE PARENTAL AND TERRITORIAL BEHAVIOR OF THE KILLDEER

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Variability in the role structure and mating systems of Charadriiformes has been extensively documented (Jenni 1974, Pitelka et al. 1974, Hildén 1975). Several papers have discussed the adaptive significance of these social systems, especially in regard to the behavioral mechanisms involved (Oring and Knudson 1972, Parmelee and Payne 1973, Graul 1974, Pitelka et al. 1974, Emlen and Oring 1977, Graul et al. 1977, Jenni and Betts 1978, Oring and Maxson 1978). Some of the latter have addressed the theoretical role of parental investment (see Trivers 1972) in explaining the ecological significance of a given mating system (Graul 1974, Emlen and Oring 1977, Graul et al. 1977). As noted by Pierotti (1981) many aspects of parental investment (as defined by Trivers 1972) are difficult or impossible to quantify. However, Pierotti (1981) and Burger (1981) quantify aspects of "parental care" for the Western Gull (*Larus occidentalis*) and the Black Skimmer (*Rynchops niger*), relating sex role patterns in parental care to the reproductive and ecological "strategies" of these species. Such is the objective of this paper, with the Killdeer (*Charadrius vociferus*) serving as the model.

STUDY AREA AND METHODS

This study was conducted during March-July 1975, May-June 1976, and from March-May 1977. The study site, approximately 4 km west of Logan, Cache Co., Utah, and 3 km east of the Little Bear River on State Highway 69, consisted of adjacent, grazed pastures of 1.15 ha and 0.18 ha, respectively.

Observations were made daily for 5 h beginning 30 min after sunrise in 1975. Observations were not made daily in 1976 and 1977 but the same temporal schedule was followed. Total observation time exceeded 400 h over the three breeding seasons. Killdeers were watched from an automobile with 7 × 35 binoculars and a 20× spotting scope at distances of less than 75 m. Behavior of the birds was monitored; behavioral units of previous workers are cited in the text and other behaviors are described as follows: The "flight chase" consisted of an aerial approach resulting in displacement of a conspecific. In the "killdeer display" the displaying bird lowered its head and pointed its bill downward; vocalizing was variable but repetitive "killdeer calling" (60-80 times per min) was always included. In the "stand off/parallel run" chasing occurred as in the "ground chase" (Phillips 1972:3-4, Fig. 2a, b, d) although no bird was clearly dominant and participants might change positions (Bunni 1959:240-244, 245). In the "preen" the subject preened in a fluffed, oblique position often orienting the cinnamon rump and back toward other birds; preening motions were quick, cursory and abbreviated. This display/comfort activity was performed on hummocks or other high places in the territory. "Deet calling" employed the *deet* vocalization (20-25 syllables per min). Bunni (1959) and Bursian (1971) considered this vocalization a contact call. In the

TABLE I
HOURS OF OBSERVATION OF MALE AND FEMALE KILLDEERS AT DIFFERENT STAGES OF
Reproduction^a

Stage ^b	Males	Females	χ^2
PN	42	38	0.20
EL	29	17	3.13
I	51	46	0.26
B	10	11	0.05
Total	132	112	1.64

^a Values were omitted for nests where the female deserted the brood after hatching. None of the observed differences between males and females was significant (χ^2 test, $P > 0.05$).

^b PN = prenesting period; EL = egg-laying period; I = incubation period; B = brooding period.

"stand/rest" the subject stood fluffed on a hummock for more than 10 min neither vocalizing nor making any conspicuous movements. The "short killdeer flight" was lower (3–6 m above the ground) and shorter (less than 30 sec) than the "killdeer flight," and only one bird was involved. Most often the bird flew in a straight line from one end of its territory to the other using slow, deep wing beats (which conspicuously displayed the white underwing), while "killdeer calling" repetitively.

Each unit was tabulated, timed with a stopwatch and related to both the stage of nesting and the sex of the participating individuals (if known). Individuals were sexed by their position in copulation (Bunni 1959, Phillips 1972). Known males and females were observed on alternate days. Table I gives the observation time for each sex at all stages of reproduction.

Eleven adults (five pairs) and 16 chicks were captured at the nest using traps modified from those designed by Coulter (1958) and by Martin (1969). All birds were banded with Fish and Wildlife Service bands and colored leg bands and uniquely dyed on various part of the plumage. Most observations prior to egg-laying were made on unmarked birds, but two Killdeers were positively identified by unusual plumage characteristics.

RESULTS

Wintering Killdeer and Early Arrivals

A few Killdeers wintered in Cache Valley. These birds tolerated close approaches (less than 3 m) by feeding conspecifics; few chases and no attacks were seen until the arrival of the migrants in early March. The migrants' presence appeared to stimulate aggression at the feeding areas. Vocalizing increased noticeably, "flight chases" occurred more frequently and feeding birds remained 30 m or more from conspecifics.

When a feeding Killdeer approached a conspecific too closely a series of "killdeer calls" was given; the "killdeer display" occurred three times under these circumstances and 22 times following territorial intrusions. In 10 of 25 observations the intruder failed to depart. In five of these 10 instances a "flight chase" ensued.

TABLE 2
NUMBER OF OCCURRENCES OF DISCRETE BEHAVIORS PER 100 H FOR MALE AND FEMALE
KILLDEERS OVER ALL STAGES OF REPRODUCTION

Behavior	Males	Females	χ^2 ^a
"Killdeer flight"	11.44	2.71	6.19*
"Ground chase"	51.81	37.05	3.00
Attack	53.82	1.81	54.77*
Scrape	39.02	15.36	11.96*
Initiate scrape	22.88	5.42	12.38*
Scrape exchange	14.13	46.99	22.26*
"Short killdeer flight"	26.24	9.04	10.15*
"Killdeer display"	16.15	3.61	9.01*
"Flight chase"	67.28	28.01	19.45*
"Stand off/parallel run"	12.18	6.33	2.24
"Deet call"	17.49	9.94	2.52

^a All comparisons are made with $df = 1$.

* Indicates a significant difference between number of occurrences for males and females at the $P < 0.05$ level.

Prenesting Period

Territory establishment and agonistic behavior.—As snow melted from pastures and open fields, male Killdeers dispersed to these areas and began to set up territories. Lone males advertised by standing in elevated sites and vocalizing (Phillips 1972:1). Advertising was interrupted by 10–20 min feeding bouts. Almost all feeding was done on the territory.

Aerial intrusion by a conspecific elicited various responses by the resident male: most commonly an increased rate of calling, but also "killdeer flights" (Phillips 1972:1, 2–3). Both males and females made "killdeer flights," although males did so significantly more often (Table 2). In nine of 11 flights in which the sexes were known both participants were male. "Killdeer flights" were most frequent during prenesting (Fig. 1a).

Persistent approaches by conspecific intruders on foot resulted in "ground chases" (Phillips 1972:3–4; Fig. 2a, b, d). "Ground chases" were frequent during prenesting (Fig. 2a) and were performed nearly equally by males and females (Table 2).

When birds were more evenly matched, a "stand off/parallel run" followed the resident's approach. "Parallel running" was punctuated by "stand offs" which lasted up to 8 min (Phillips 1972:4–5). Typical sequences involved from 2–10 "parallel runs" and as many "stand offs." Any bird could attack another during a "stand off/parallel run" sequence. Females were much less likely to attack than males (Table 2; Fig. 2b), and the frequency of female-initiated attacks and "ground chases" decreased markedly as egg-laying approached.

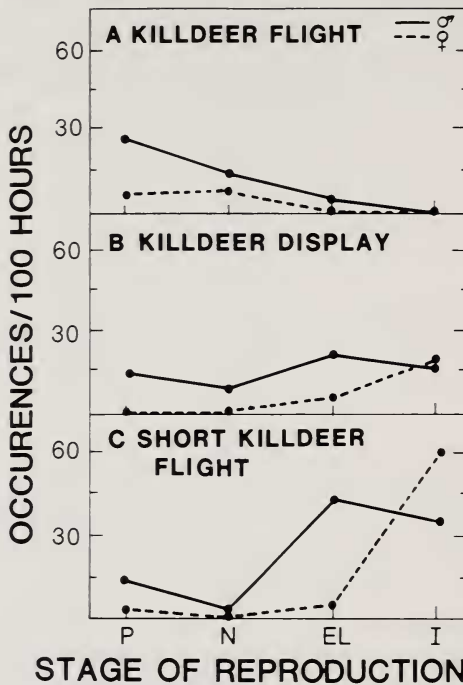


FIG. 1. Comparison of the rate of occurrence of three discrete behaviors for male and female Killdeers at four stages of the reproductive cycle. PN = prenesting period; EL = egg-laying period; I = incubation period; B = brooding period.

Females residing on established territories reacted to intruders in different ways than males. They employed less overtly aggressive displays. In response to an intruder the female resident usually moved to a nearby elevated area of the territory and "deet called" for 30 sec-2 min. If the intruder remained, the female approached in run/stop fashion, "deet calling" and sometimes "killdeer calling." As she neared the intruder, stops were more frequent and included pecking and tossing as well as short (1-4 min) bouts of preening. No female alone on the territory ever chased or attacked an intruder. The female resident preened at closest approach to the intruder.

The return of the male resident preceded "killdeer flights," "ground chasing," "stand off/parallel runs" or even attacks involving the resident male and the intruder. The returning male was apparently attracted to the site of the intrusion by the calls of the female. Resident females joined in "killdeer flights" and "stand off/parallel runs" only in the presence of their mates. Such participation declined markedly as egg laying approached.

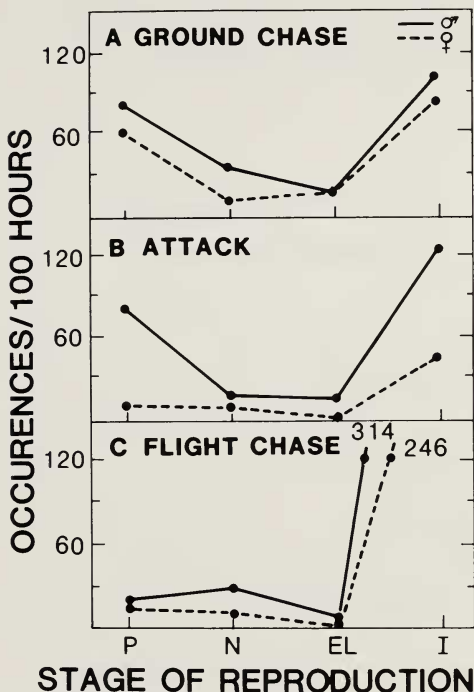


FIG. 2. Comparisons of the rate of occurrence of three discrete behaviors at four stages of the reproductive cycle. Abbreviations as in Fig. 1.

Territorial males advertised to females by scraping (Phillips 1972:1-2; Fig. 1c). Lone territorial males scraped in bouts lasting 2-20 min. Scraping is performed almost exclusively during prenesting and egg-laying and more frequently during the former (Fig. 3c). Males spent more time scraping than females ($t = 12.11$, $df = 61$, $P < 0.05$), except during egg-laying, and scraped significantly more often (Table 2, Fig. 3c).

Unpaired females are attracted to a scraping male and enter the potential nest-site in a complex ritualized display called the "scrape exchange" (Phillips 1972:5). Males initiated scraping in most instances; the female entered after the display had begun (Table 2, Fig. 3a, b).

Males limited their activity to their own territories. Females roamed over the territories of two or more males before pair formation. Males continued to scrape and vocalize even after they had paired, often attracting unmated females. These birds were driven off by the resident female. In seven of 22 total "ground chases" made by females, the chased bird was also a female, in another seven of these "ground chases" the chased bird was presumed to be a female because the resident male scraped or

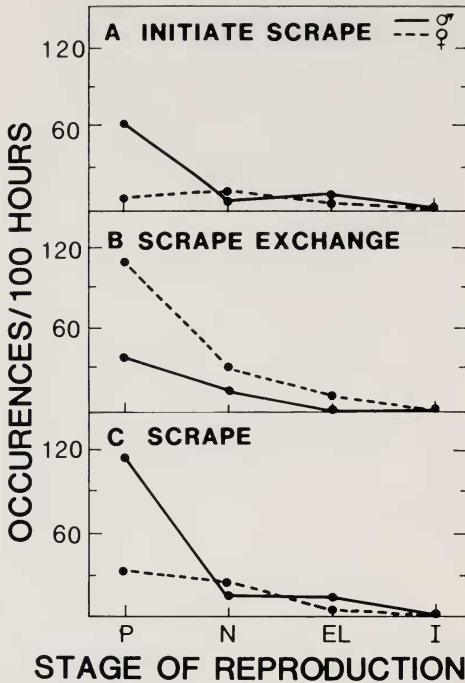


FIG. 3. Comparisons of the rate of occurrence of three discrete behaviors at four stages of the reproductive cycle. Abbreviations as in Fig. 1.

directed precopulatory approaches toward it; in the remaining eight of 22 female "ground chases" the chased bird was of unknown sex. In some of these chases the resident male also chased. In two of two attacks made by females the recipient was presumed to be a female because the resident male directed precopulatory approaches at it (the recipient).

Three mated birds copulated with birds other than their mates (Mundahl 1977). In all cases the intruding females approached the resident males when the resident female was distant; all occurred during prenesting.

Egg-laying Period

This period began when the first egg was found, or by backdating to the first egg (Bunni 1959) and ended when the complete clutch was laid.

Territory defense and agonistic behavior.—Aggressive displays used in defense of the territory were the same as those used during prenesting but their rates diminished to less than 50% of the values during prenesting (Figs. 1a, 2a, b) for both sexes combined. These decreases were significant for "ground chases" ($\chi^2 = 10.09$, $df = 1$, $P < 0.05$) and attacks ($\chi^2 = 11.87$, $df = 1$, $P < 0.05$).

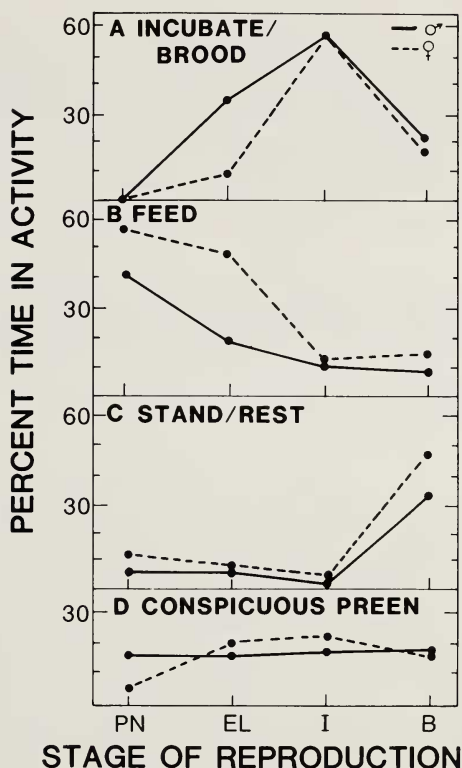


FIG. 4. Percent of time spent in four continuous behaviors by male and female Killdeers as a function of the stage of reproduction. Abbreviations as in Fig. 1. Percent values were obtained by determining the total amount of time spent by each sex in a behavior during a given stage of reproduction, dividing by the total observation time for that sex in that stage and multiplying by 100.

Nest building.—Both sexes spent significantly less time scraping during egg-laying than during the prenesting period (males: $t = 1.97$, $df = 28$, $P < 0.05$; females: $t = 2.90$, $df = 31$, $P < 0.05$).

Incubation.—Males spent more than three times as much time incubating as females during egg-laying (Fig. 4a).

Feeding.—Females spent more than twice as much time feeding as males during egg-laying (Fig. 4b) and overall (Table 3).

Incubation Period

Territory defense and agonistic behavior.—Phillips (1972) found aggression levels high during incubation, but in this study overt aggressive displays were markedly lower during incubation than at other times (Figs. 2a, b, c). “Ground chases” ($\chi^2 = 26.29$, $df = 1$, $P < 0.05$) and attacks

TABLE 3
COMPARISON OF MEAN DAILY PERCENT OF TIME INVESTED BY MALE AND FEMALE
KILLDEERS IN CONTINUOUS BEHAVIORS OVER ALL STAGES OF REPRODUCTION^a

Behavior	Comparison bias ^b	df	t
Feed	Female	125	2.280*
Distraction	Male	127	2.525*
Stand/rest	Female	124	0.564
Conspicuous preen	Male	126	0.695

^a Daily proportion values were transformed using the inverse standard normal cumulative distribution as described by Romesburg (1976). Paired, two-tailed *t*-tests were performed using the transformed variates. This method and the arcsin transform method described by Sokal and Rohlf (1969) agreed with respect to both showing significance or non-significance 90% of the time.

^b Sex which spent the greatest mean daily proportion of time in the behavior indicated.

* Indicates a significance difference at the $P < 0.05$ level.

($\chi^2 = 27.67$, $df = 1$, $P < 0.05$) declined significantly compared to pre-nesting values. The mean daily percent of time spent "stand off/parallel running" shows a significant decline from egg-laying to incubation (males: $t = 6.49$, $df = 62$, $P < 0.05$; females: $t = 3.31$, $df = 59$, $P < 0.05$).

During inattentive periods birds foraged and preened off the territory. Intrusion by a conspecific in a remote area of the territory elicited an approach by the resident, usually followed by a bout of preening; the intruder almost always retreated. The "killdeer display" (Fig. 1b) and "short killdeer flight" (Fig. 1c) increased in rate for both sexes during incubation. These displays were shorter and seemed less overtly aggressive than the "ground chases," attacks and "killdeer flights" employed earlier.

Incubation and nest defense.—The sexes shared incubation nearly equally during the daylight hours (Fig. 4a). However, males seemed to perform most nocturnal incubation. I trapped one bird from each of four marked pairs on the nest on five different nights at 21:30, 22:00, 01:00, 01:00, and 05:30; all were male. In addition, I observed three marked pairs (10 days–3 weeks into incubation) on six consecutive evenings. The male initiated incubation before dusk and no incubation exchanges were made by night-fall. Time spent at the nest increased during incubation for both sexes (Fig. 4a). Females were more reluctant to approach a disturbed nest. Trapping success at the nest was 89% for males and 35% for females.

The presence of a predator elicited rapid "deet calling" from the inattentive bird. One or both birds began to distract the predator. Distraction behavior occurred during prenesting but increased significantly for males after the eggs were laid ($t = 2.69$, $df = 64$, $P < 0.05$). Males spent significantly more time distracting than females (Table 3).

Brooding Period

Agonistic activities.—The most conspicuous features of the brooding period were the cessation of the boundary defense of the nesting territory and the increased intraspecific aggression, especially by females. As soon as the clutch hatched, resident Killdeers ceased defending areas of their nesting territory and only defended an area around their brood varying in radius from 20–40m.

Behavior was similar to that employed in territorial establishment during prenesting. Pronounced increases in the rates of “ground chases” (Fig. 2) are statistically significant for both sexes (males: $\chi^2 = 17.50$, $df = 1$, $P < 0.05$; females: $\chi^2 = 9.71$, $df = 1$, $P < 0.05$) and increases in attacks were statistically significant for males ($\chi^2 = 64.02$, $df = 1$, $P < 0.05$; females: $\chi^2 = 2.73$, $df = 1$, $P < 0.05$). Females were considerably more aggressive during brooding than previously.

The “flight chase” was the most frequent method of repelling conspecifics during brooding (Fig. 2c). The difference in the rate of flight chasing between incubation and brooding was statistically significant for both sexes (males: $\chi^2 = 155.73$, $df = 1$, $P < 0.05$; females: $\chi^2 = 43.74$, $df = 1$, $P < 0.05$). Figure 1c shows the increase in “short killdeer flights” during brooding for females: this display advertised the presence of the pair and was less time consuming than the “killdeer flight.”

Brooding.—Attentive birds were very conspicuous during brooding. They kept contact with the brood by remaining stationary and “deet calling” continuously during early mornings and late evenings though less in midday. Males and females spent similar proportions of time “deet calling” during brooding ($t = 0.11$, $df = 16$, $P < 0.05$). Males spent about the same amount of time brooding as females (Fig. 4a; excluding one of three successful pairs in which the females deserted).

Female desertion.—The only marked female to hatch a second clutch deserted immediately after hatching, but two marked females that produced successful first clutches were attending their broods 12 days after hatching when I terminated my observations.

DISCUSSION

Trivers (1972) defined parental investment as “any investment by the parent in an individual offspring which increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring.” Trivers (1972) believed that in monogamous bird species, females invest slightly more in a single clutch than males. To rigorously test Trivers’ (1972) hypothesis would require information on energy expenditures as well as the effects of given behavior

patterns on future reproductive success. Such information is difficult to obtain in a field study. However, quantitative data on parental care can be obtained (Burger 1981, Pierotti 1981) and certainly represent a type of parental investment which will affect the ecological success and mating strategies of the sexes within a given species.

My data on parental care indicate that the degree of role specialization practiced by Killdeers tends to equalize the parental investment by each sex over a given breeding season. For brevity and convenience I follow Trivers (1972) in employing the language of reproductive strategy in explaining what adaptations natural selection would be expected to favor.

In Killdeers both sexes incubate, brood, and show similar agonistic behaviors. The degree to which role specialization occurs appears to be dictated by the reproductive energy demands for each of the sexes. As noted by King (1973) and Ricklefs (1974) female birds produce gametes with a large amount of stored energy, whereas the male's energy expenditure in gamete production is minimal. Since female Killdeers lay eggs in rapid sequence (nearly an egg per day, on the average) (Furniss 1933, Bunni 1959), and frequently replace clutches (Bunni 1959), their energy demand for oogenesis must be considerable. Accordingly, the females' behavior prior to incubation should tend to minimize energy expenditures not related to gamete production while increasing those activities which contribute to successful production of eggs.

Since food deprivation produces a more severe depression of reproductive output in female birds than in males (Assenmacher et al. 1965, King 1973, Ricklefs 1974), it would seem advantageous that male Killdeers assume the metabolically more costly tasks of nest-building, territory defense, and incubation during prenesting and egg-laying while females are mobilizing energy for egg production or recuperation from egg production.

Prenesting and Egg-laying Periods

Agonistic and territorial behavior.—In this study the female Killdeer's role in territorial establishment was shown to be minimal. Males performed "killdeer flights," "short killdeer flights," and scraping displays significantly more often than females (Table 2). These displays are conspicuous visually and acoustically and probably serve to communicate the performer's presence as a form of territorial advertisement.

The female Killdeer's role in territorial defense was one of secondary importance. Males made significantly more "killdeer displays," "flight chases," and attacks than females (Table 2; Figs. 1b; 2b, c); these displays are aggressive. Attacks may expose the attacker to retaliation or involvement in prolonged fighting representing a potentially large energy investment or increased risk of predation during fighting. Jaeger (1981) conclud-

ed that attacks between red-backed salamanders (*Plethodon cinereus*) could inflict injuries which would impair the opponent's biological fitness. During prenesting and egg-laying, females chased intruders of unknown sex only when their mates also chased.

Paired female Killdeers seemed to restrict overt aggressive activities to encounters with other females during early prenesting; they also performed more passive displays which could discourage intrusion of the territory by other females. Females and males employed the "stand/rest" and "preen" about equally during the discrete stages of reproduction (Fig. 4c, d) as well as throughout the reproductive cycle (Table 3). Although these are not overtly aggressive displays, Geist (1974) concluded that in a monomorphic species the presence of an individual of either sex discourages trespass of territory.

The increase in the proportion of time spent feeding (Fig. 4b) and the decrease in the occurrence of aggressive actions by female Killdeers near the end of prenesting suggest that they were mobilizing maximum energy for egg production at that time.

Male reproductive strategy and mate defense by females.—Phillips (1972) noted a case of a male Killdeer directing precopulatory behavior toward a strange female near his nest and suggested that males could respond to females even late in incubation. In this study, males directed precopulatory displays toward any female that was present. If the male's mate returned while another female was present, he then assisted the resident female in chasing the intruder away.

As noted by Trivers (1972), the optimal breeding strategies of the two sexes are rarely identical. The male maximizes his fitness by inseminating as many females as possible. However, the male can also increase his fitness by caring for his eggs and young and by defending his territory, and can be expected to exhibit a high degree of territorial and parental behavior. A more extreme example of this two-pronged male strategy occurs in the Mountain Plover (*Charadrius montanus*) in which at least some males mate with one female and assume all incubation duties for that female's clutch but remain sexually active (Graul 1974). In species in which male parental investment is large, the female maximizes her fitness by defending her mate from potential competitors (Orians 1969). Tinbergen (1939) stressed the importance of female-female aggression in the Snow Bunting (*Plectrophenax nivalis*) in maintaining monogamy in that species. Morton et al. (1978) quantified aggressive responses of female Eastern Bluebirds (*Sialia sialis*) to models of female conspecifics and postulated that the high levels of aggression serve to ensure a paired female of maximum continued investment from her mate after she has laid. Graul (1974) noted that in the Mountain Plover males tend to react aggressively toward

males and females behave aggressively toward females. In the Killdeer, female-female aggression probably serves to stabilize the pair bond.

An inseminated female whose mate has deserted her and remated faces a larger energy investment if she must care for the clutch/brood unaided. In the long run, the female may conserve energy by defending her mate from competitors, thus ensuring that he will contribute to the rearing of the young.

The most common forms of aggressive behavior witnessed in female-female encounters were the "ground chase" and the "flight chase." Figure 2a, c show that the frequency of occurrence of "ground chases" and "flight chases" by females closely parallel the frequency of occurrence of the same behaviors by males at each stage of the reproductive cycle. These displays convey a high likelihood of attack and should be efficient for repelling intruding females. Except for brooding, the rates of occurrence of these behaviors are highest during prenesting and during prenesting these displays are most often directed at other females. Mate defense is probably most critical during prenesting when many potential competitors are yet unmated.

The advantages of extra-pair copulation by mated females of monogamous bird species were reviewed by Gladstone (1979). In this study one of three females involved in non-monogamous copulation appeared to be already paired with a male; the other two females could not be positively identified.

Incubation Period

Incubation and brood defense.—Norton (1973) estimated the heat requirement in the Dunlin (*Calidris alpina*) at 120% of BMR using Kendeigh's (1963) equation. Ricklefs (1974) and Kendeigh (1973) contended that the energy requirement for incubation must be supplied largely by supplemental heat production, especially in open-nesting species, but King (1973) believed that incubation entailed no additional cost. I have presented evidence that the male Killdeer performs most (or all) of the night incubation. At night the energy cost would be higher than during the day, especially early in the breeding season. Night incubation by the male leaves the female free to feed, seek shelter, and reduce energy expenditure during this time. The incubating bird may also increase its investment by rendering itself more susceptible to predation by incubating at night (Burger 1974; T. A. Sordahl, pers. comm.).

Distraction behavior is believed to enhance the survival of the eggs or young by directing a potential predator's attention toward the parent bird. A bird may render itself more vulnerable to predation or injury by displaying closer to or even attacking the predator (Smith 1969, Myers 1978,

Denson 1979). Table 3 shows that males spent significantly more time giving distraction displays than females on a mean time per day basis. The male's investment in clutch and brood defense is thus greater than that of the female. Likewise, the female Killdeer's hesitation to approach a disturbed nest may render her less susceptible to predation at the nest than the male.

Brooding Period

Agonistic behavior and brood defense.—Females and males markedly increased their rates of display and aggressive activities during the brooding period (Figs. 1b; 2a, b, c). The increase in display and agonistic activity by the female seems paradoxical unless viewed as a means by which the fitness of the parent is maximized. Once a clutch has hatched, aggressive brood defense is probably selected for, rather than conservation of energy for possible replacement of clutches. Mace (1971) presented data which suggest that fledging success is higher than hatching success in Killdeers. Defense of the brood during this period may provide high returns in reproductive success. There is also less time to produce another brood.

Göransson et al. (1975) demonstrated that the aggressive behavior of Northern Lapwings (*Vanellus vanellus*) decreased the predation rate on artificial lapwing nests placed in lapwing territories relative to those placed outside their breeding territories. Kruuk (1964) believed that attacks by Common Black-headed Gulls (*Larus ridibundus*) on potential predators improved the chances for successful hatching of the gulls' young. The increase in aggression of female Killdeers during brooding probably increases the chances of chick survival.

Desertion by females.—Several workers have noted that it is common for female Killdeers to desert the brood shortly after hatching (Bunni 1959; R. E. Phillips, pers. comm.; Mundahl, pers. obs.), especially late in the breeding season. This phenomenon has been reported for other monogamous shorebirds (Lenington 1980). The potential adaptive advantages of Killdeer female desertion are treated by Lenington (1980), who suggested that female Killdeers deserted when physiologically taxed by the stress of egg production. Perrone and Zaret (1979) also suggested that differences in the ability of the parents to provide parental care may dictate which sex is most likely to desert.

SUMMARY

The behavior patterns of the Killdeer (*Charadrius vociferus*) during the nesting cycle are reviewed. The frequencies of occurrence of discrete behaviors were monitored for each sex during the prenesting, egg-laying, incubation, and brooding periods and are compared graphically. Continuous behavior patterns were timed, and the total and average amounts of time

spent performing these behavior patterns were compared for male and female Killdeers during these four stages of the breeding cycle.

The roles of breeding male and female Killdeers are discussed with emphasis on the energetic demands and reproductive strategies of each sex. I propose that male Killdeers tend to compensate for the large energy investment of the female by taking a greater part in territorial establishment and defense, parental behavior, and nest and brood defense. The male assumed the major role in territorial establishment and defense during the prenesting and egg-laying period. The female defended her mate from other females through egg-laying but her role in territory defense was limited to passive displays, whereas the male manifested intolerance of intruders by active displays, chasing, and attacks. The male also assumed the major role in nest building and incubation. The greater proportion of time spent distracting by males and probable higher proportion of night incubation by males may represent higher parental investment due to increased risk of predation.

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